

Reappraisal of plumage and morphometric diversity in Thick-billed Grasswren *Amytornis modestus* (North, 1902), with description of a new subspecies

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Received 14 December 2015

SUMMARY.—Morphological, distributional, ecological and genetic studies distinguish seven subspecies within Thick-billed Grasswren *Amytornis modestus*. One, newly described here from the Sturt Stony Desert in north-eastern South Australia, is the palest and least streaked, and has a relatively short bill and wings. It is estimated to be Vulnerable under IUCN criteria with a known Extent of Occurrence of <1,500 km². Two subspecies are extinct and one is Critically Endangered. Parapatry has been recognised recently between two genetically divergent subspecies but all of the others are presently inferred to be allopatric.

Thick-billed Grasswren *Amytornis modestus* is one of 11 presently recognised species within the purely continental Australian genus *Amytornis* (Black *et al.* 2010, Christidis *et al.* 2010). The species once ranged across arid central and semi-arid south-eastern Australia in up to eight largely allopatric populations (Black *et al.* 2010, 2011, Black 2011a) (Fig. 1). Grasswrens are very specific in their habitat requirements (Rowley & Russell 1997, 2007) and, while most are dependent upon 'spinifex' tussock grasslands, Thick-billed Grasswren is almost entirely restricted to chenopod low shrublands, generally in depressions and drainage lines on stony plains. Two of five subspecies of its sister species Western Grasswren *Amytornis textilis* also occupy (or occupied) chenopod low shrublands (Black 2011b).

Among the eight populations of *A. modestus* there are six named subspecies and one population that is not formally named. A phylogenetic study, sequencing mitochondrial DNA (ND2) (Austin *et al.* 2013), found a clade of western distribution comprising the first two subspecies named below, each constituting an almost monophyletic haplogroup. Net DNA divergence between that clade and another (eastern) clade was 1.7%. The second clade contained four allopatric populations (3–6 below), none monophyletic but each with unique haplotypes, the pattern indicating incomplete sorting between more recently diverged lineages. Estimated time to most recent common ancestor was c.0.11 MYA, i.e. towards the end of the last interglacial (Fig. 1). Morphological and plumage distinctions among the eight populations, presented below, are taken from Black (2011a) with habitat data from Black *et al.* (2011) unless otherwise qualified. Their known or inferred historical distributions are shown in Fig. 2.

- (1) *Amytornis m. modestus* (North, 1902). The unique and atypical habitat of the long-tailed, relatively dark but lightly streaked nominate subspecies, now extinct, was Sandhill Canegrass *Zygochloa paradoxa* along the sandy beds of watercourses within the mountains of central Australia, in Northern Territory (NT) (Whitlock 1924, Black 2012).
- (2) *A. m. indulkanna* (Mathews, 1916). The closely related (Austin *et al.* 2013) but paler and much shorter tailed subspecies of the western Lake Eyre basin in South Australia (SA) occurs chiefly in low shrublands of Oodnadatta Saltbush *Atriplex nummularia omissa* or Cottonbush *Maireana aphylla*.

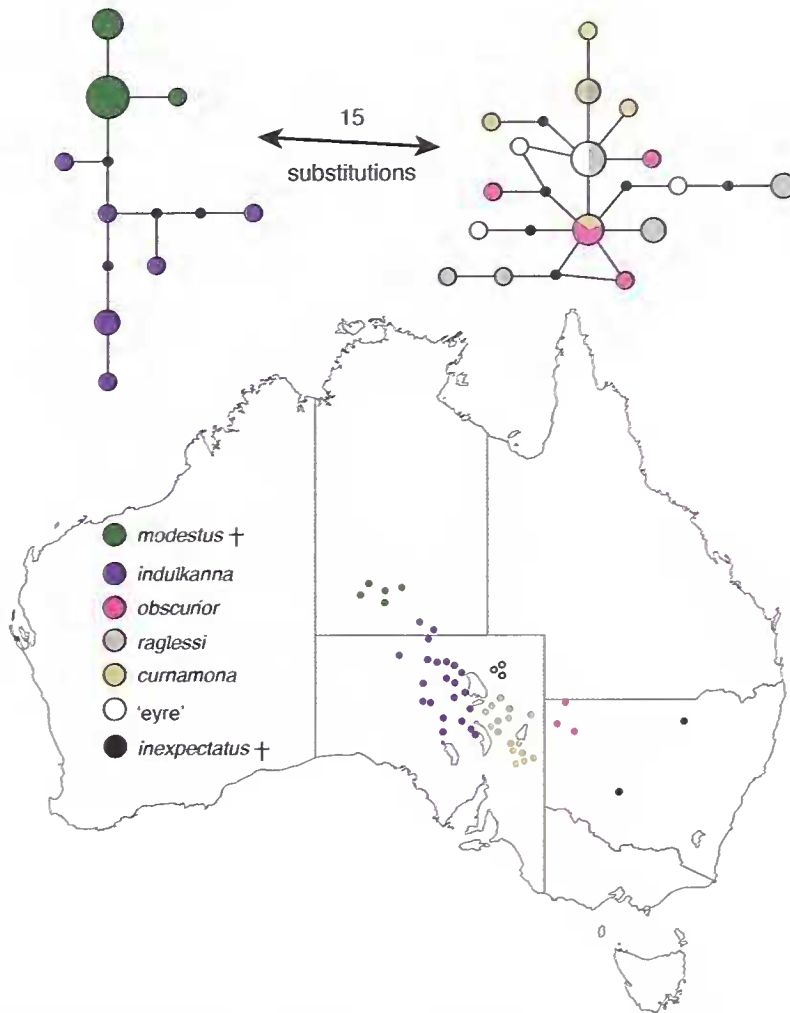


Figure 1. Map of Australia, showing occurrence of Thick-billed Grasswren *Amytornis modestus* subspecies with the unrooted mitochondrial DNA (ND2) network, after Austin *et al.* (2013).

(3) *A. m. raglessi* Black, 2011, of the North Flinders Ranges (SA) periphery belongs to a separate (eastern) clade, but is phenotypically very similar to *A. m. indulkanna* other than, on average, having a longer tail. Its habitats are low shrublands of Blackbush *Maireana pyramidata* and less frequently Low Bluebush *Maireana astrotricha*. Genetic divergence between the two clades (Austin *et al.* 2013) suggests their vicariance across the Eyrean Barrier (Ford 1987, Schodde & Mason 1999) during the late Pleistocene (c.0.36 MYA).

(4) *A. m. curnamona* Black, 2011, of the southern Lake Frome basin (SA) is darker and longer tailed than *A. m. raglessi* and is largely restricted to Blackbush low shrubland but occurs infrequently in low shrublands of Spiny Saltbush *Rhagodia spinescens* and Australian Boxthorn *Lycium australe*.

(5) *A. m. obscurior* (Mathews, 1923) of the Grey Range periphery in north-western New South Wales (NSW), long considered extinct, was rediscovered in 2008 in a tiny and highly endangered population (Parker *et al.* 2010) that occurs in Blackbush and Cottonbush low shrublands (AB pers. obs.).

(6) *A. m. 'eyre'*. The fourth population within the eastern clade occupies a limited range in the stony plains east of Lake Eyre (SA), within a partially resolved drainage into

the Warburton River below Goyder Lagoon in the Diamantina River system (Fig. 7). Its habitats are Old-man Saltbush *Atriplex nummularia nummularia* shrubland and low shrublands of Cottonbush, Oodnadatta Saltbush and Spiny Saltbush. It has not been formally described.

(7–8) *A. m. inexpectatus* (Mathews, 1912). Only one specimen representing this subspecies is held in an Australian museum and it proved uninformative in the DNA sequencing study of Austin *et al.* (2013). It was described from two separate populations >400 km apart in eastern NSW. Habitats occupied by these long-extinct populations have not been confidently determined but were probably chenopod or Nitrebush *Nitraria billardierei* shrublands or low shrublands (Parker 1972, McAllan 1987).

An earlier morphological review of the species (Black 2011a) examined four of the above subspecies (epithets used hereafter for simplicity), *modestus*, *indulkanna*, *raglessi* and *curnamona*, while the phylogenetic study (Austin *et al.* 2013) included the same four plus *obscurior* and 'eyre'. Subsequent examination of specimens of *inexpectatus* in North American and European museums (Black *et al.* 2014) now provides an opportunity to reappraise plumage and morphological diversity within the species as a whole.

This review will include the unnamed 'eyre' population, represented by a small number of museum specimens, and will provide its formal description and name. Only two specimens are available of the now Critically Endangered population of *obscurior* and the only adult male (in the Mathews collection, American Museum of Natural History, New York) was included within the review.

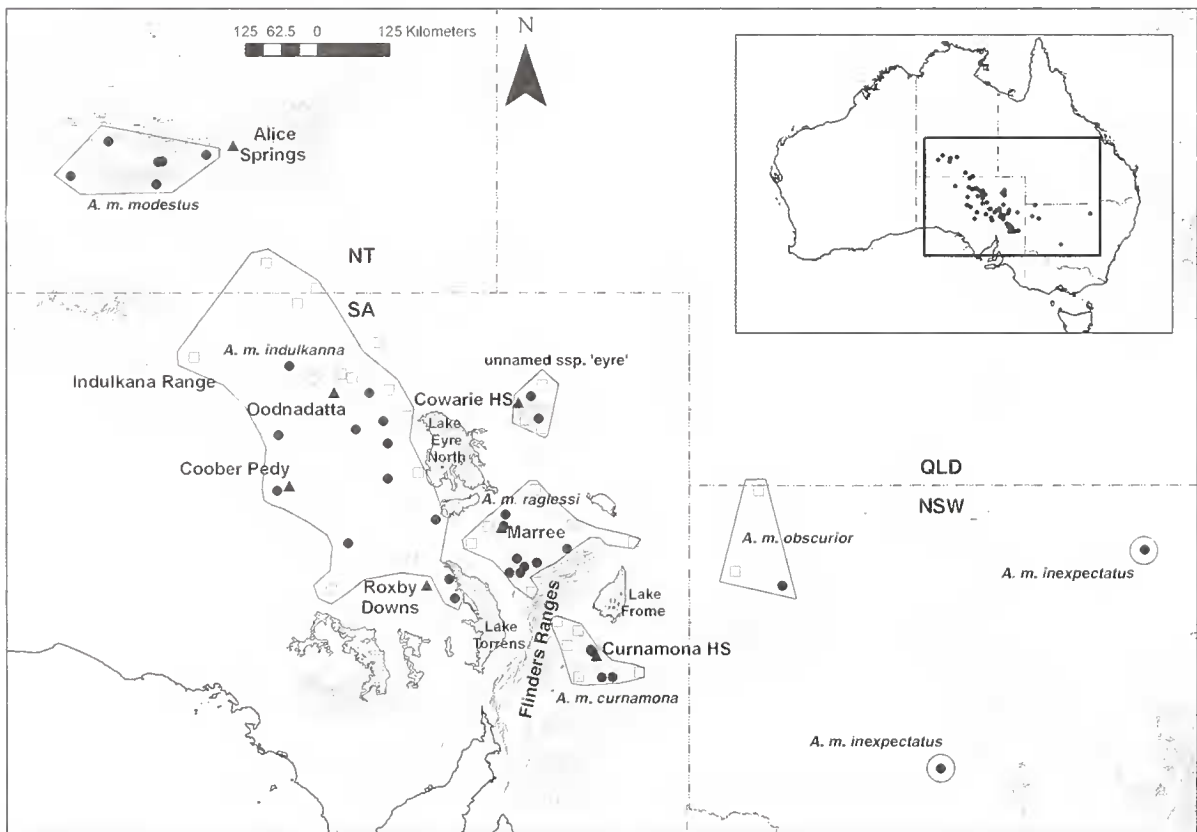


Figure 2. Map of central and inland south-eastern Australia, showing the distribution of Thick-billed Grasswren *Amytornis modestus* subspecies. Specimens included in this study are represented as closed circles, other distributional records as open squares, after Black (2011a).

Methods

Methods follow those employed in the earlier review (Black 2011a) of morphometry and plumages of *A. modestus* material in Australian museum collections. Sampled in that review were 51 specimens: six male and six female *modestus*, nine male and four female *indulkanna*, 11 male and ten female *raglessi*, and three male and two female *curnamona*. Four morphological parameters assessed were bill length (from the junction of skull and culmen to tip), bill depth (at the point of frontal feathering), wing length (max. flattened chord) and tail length (the central rectrix from its point of emergence to tip). Statistically significant differences were found in the tail length of males. Female sample sizes were small and comparisons proved statistically uninformative. The same four subspecies were tested further using factor analysis after quantifying two plumage characteristics—depth of dorsal tone and strength of ventral streaking—and each was found to be reciprocally diagnosable.

The present study involved a comparative analysis of 42 male specimens of all seven subspecies, including the unnamed 'eyre'. Sample sizes of specimens with complete data were: *modestus* ($n = 7$), *indulkanna* ($n = 9$), *raglessi* ($n = 11$), *curnamona* ($n = 3$), 'eyre' ($n = 4$), *obscurior* ($n = 1$) and *inexpectatus* ($n = 8$).

In distinguishing all subspecies, the measured parameters (as above) were first compared between subspecies within each of the two established genetic clades, using univariate parametric statistics. Within the eastern clade, the largest sample (*raglessi*, $n = 11$) was used primarily as the statistically most applicable comparator. The moderately well collected but genetically unsampled *inexpectatus* ($n = 8$) was compared to subspecies with the closest values. Subsequently, the combined morphometric data were tested using factor analysis. In the present study, the qualitative plumage variables—depth of tone and strength of ventral streaking—were considered independently.

Results

Measurements of wing and tail length plus bill length and depth of males of seven subspecies are presented in Table 1. The results of factor analysis of all seven subspecies are shown in Fig. 3. Factor 1 largely reflects bill depth and relative bill 'thickness', and factor 2

TABLE 1
Morphometrics of seven subspecies of Thick-billed Grasswren *Amytornis modestus*. Asterisks indicate statistically significant parameters referred to in the text.

Subspecies	<i>n</i>	wing	tail	bill length (L)	bill depth (D)	L/D
<i>modestus</i> mean ± SD	7	62.1 ± 1.7	80.8 ± 2.5 *	12.6 ± 0.7	6.2 ± 0.3	2.0 ± 0.1
range		59–64	76.1–83.6	11.3–13.5	5.9–6.9	1.8–2.2
<i>indulkanna</i> mean ± SD	9	60.0 ± 3.0	69.5 ± 2.9	13.3 ± 0.7	6.1 ± 0.3	2.2 ± 0.1
range		57–66	65.1–73.8	12.2–14.4	5.8–6.6	2.1–2.3
<i>raglessi</i> mean ± SD	11	61.3 ± 1.8	74.5 ± 2.8	13.1 ± 0.6	6.3 ± 0.2	2.1 ± 0.1
range		59–64	69.3–77.8	11.9–13.7	5.9–6.6	1.9–2.3
<i>curnamona</i> mean ± SD	3	61.0 ± 2.6	78.1 ± 0.6 *	13.2 ± 1.4	6.2 ± 0.4	2.1 ± 0.1
range		58–63	77.6–78.8	12.2–14.8	5.8–6.5	2.0–2.3
'eyre' mean ± SD	4	58.3 ± 1.0 *	72.9 ± 2.5	12.0 ± 0.3 *	6.1 ± 0.4	1.9 ± 0.1
range		57–59	70.6–76.5	11.7–12.2	5.6–6.6	1.8–2.1
<i>obscurior</i> mean ± SD	1	61	80	12.9	6.1	2.1
range		61	80	12.9	6.1	2.1
<i>inexpectatus</i> mean ± SD	8	62.1 ± 3.4	82.7 ± 4.2 *	12.6 ± 0.9	5.4 ± 0.3 *	2.3 ± 0.2
range		57–68	79.5–91.2	11.3–13.6	5.0–5.9	2.0–2.5

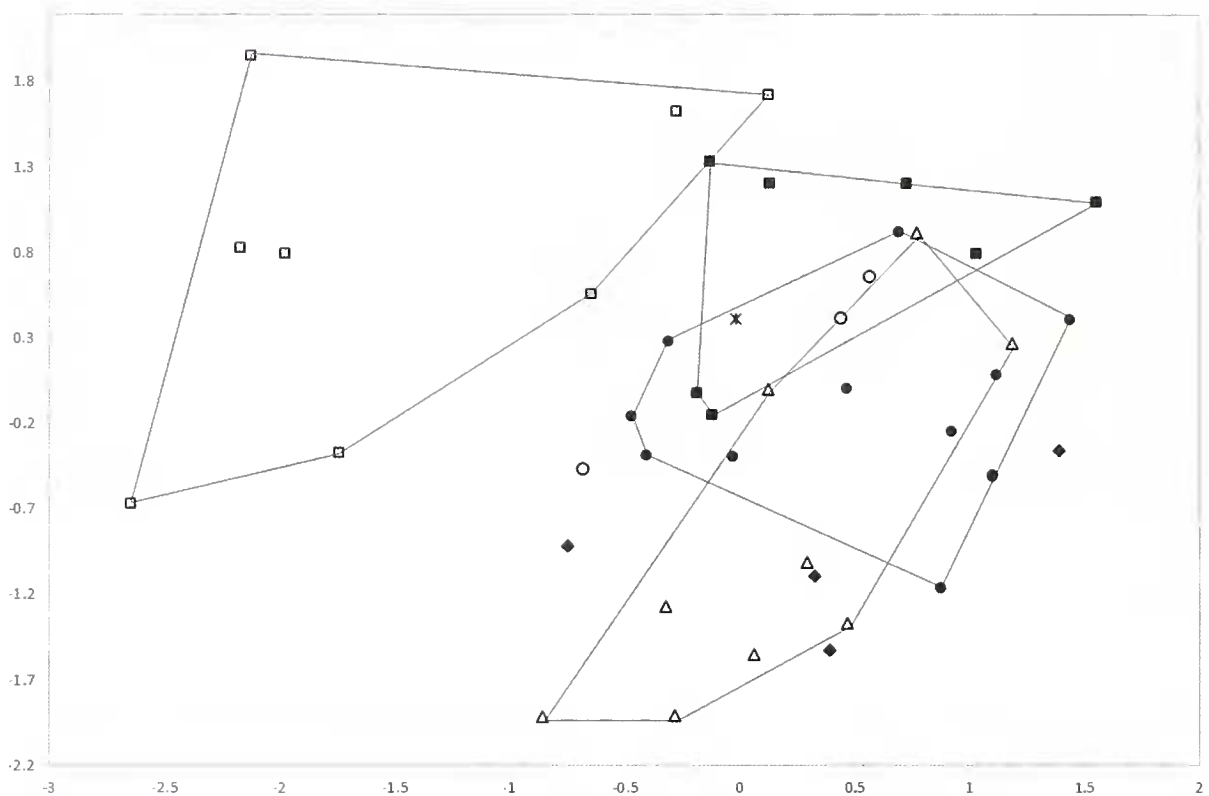


Figure 3. Factor analysis of the seven subspecies of Thick-billed Grasswren *Amytornis modestus*: *A. m. modestus* = closed squares, *A. m. inexpectatus* = open squares, *A. m. indulkanna* = open triangles, *A. m. raglessi* = closed circles, *A. m. curnamona* = open circles, *A. m. obscurior* = star and 'eyre' = closed diamonds. Loadings for factor 1 (horizontal axis) are bill depth 0.584 and length /depth ratio -0.434; for factor 2 (vertical axis) wing 0.626 and tail 0.563.

reflects wing and tail lengths. The non-metric variables dorsal tone and strength of ventral streaking are illustrated in Figs. 4–6 and discussed further below.

Discussion

Black (2011a) described distinguishing character states of plumage variables for subspecies *modestus* (darker above, very lightly streaked below), *indulkanna* and *raglessi* (pale and lightly streaked) and *curnamona* (darker and more heavily streaked). The 'eyre' population is paler than all of the named subspecies (Figs. 4–5), except perhaps *obscurior* which, from observations of live birds in the hand, may be almost as pale, but appears relatively darker on the head (Fig. 6). Because subspecies *obscurior* is unrepresented in Australian collections and *inexpectatus* by only a single historical example, direct comparison between those two and other subspecies has not been practicable. Nevertheless, specimens in overseas collections of the latter extinct subspecies appear, while taking into account dulling and browning with age, darker and more heavily streaked than most other subspecies (Black *et al.* 2014) and perhaps most closely resemble the *curnamona* phenotype in these respects.

Univariate analysis revealed that, within the western clade, its two subspecies *modestus* and *indulkanna* are reliably separated by tail length, with no overlap ($p = 0.0001$), the first-named being the second longest-tailed within the species and the latter among the shortest. In the eastern clade of four subspecies, tails of *curnamona* are longer than both *raglessi* ($p = 0.046$) and 'eyre' ($p = 0.018$), and the tail of the single *obscurior* specimen is longer than any of the specimens of the other three. Compared with others in the same clade, 'eyre' is short-

Figure 4. Dorsal view of four subspecies of Thick-billed Grasswren *Amytornis modestus*, from left to right: SAMA B55670 *A. m. indulkanna*; SAMA B55666, the similar but genetically divergent *A. m. raglessi*; SAMA B55710, the dark-plumaged *A. m. curnamoma*; and SAMA B56067, holotype of the pale newly described *A. m. cowarie* (© P. Gower)



Figure 5. Ventral view of the same specimens as in Fig. 3, showing variation in the strength of ventral streaking (© P. Gower)



winged and short-billed (cf. *raglessi* $p = 0.008$ and $p = 0.004$, respectively). Outside the two recognised clades, the genetically unsampled subspecies *inexpectatus* is even longer tailed than nomino-typical *modestus* ($p = 0.0001$) and is relatively slender billed (cf. 'eyre' $p = 0.007$). Factor analysis (Fig. 3) revealed that the easternmost subspecies *inexpectatus* separates from all others, principally on account of its being the longest tailed and least 'thick-billed'.



Figure 6. Male of the Critically Endangered subspecies of Thick-billed Grasswren *Amytornis modestus obscurior* (© L. P. Pedler)

In the western clade, *modestus* and *indulkanna* are almost mutually exclusive. Individual subspecies of the eastern clade are separated incompletely, the larger *raglessi* sample partly overlapping *curnamona* and the single *obscurior* sample, both of those being longer tailed, but largely excluding 'eyre,' which is shorter winged and shorter billed.

Black *et al.* (2011) examined the distribution of four Thick-billed Grasswren subspecies in South Australia and suggested that all were allopatric, with most separated by distances of c.100–200 km. The smallest inferred separation was between the most genetically divergent subspecies *indulkanna* and *raglessi*, where the closest known records were just c.60 km apart. Those subspecies have now been shown to be parapatric and intergradient (A. Slender pers. comm.), indicating population expansion, most likely of the first-named subspecies, subsequent to their postulated late Pleistocene vicariance. With this exception, the closest subspecies are now 'eyre' and *raglessi*, with known outlying records c.110 km apart and separated by dune fields of the Simpson-Strzelecki Desert complex and the Lower Cooper Creek floodplain. The former region is occupied by another member of the genus, Eyrean Grasswren *A. goyderi* (Fig. 7). Extinct *A. m. modestus* of central Australia (NT) appears also to have been allopatric, separated from *A. m. indulkanna* by 100–200 km (Black 2012). The two eastern subspecies, *obscurior* and *inexpectatus*, are even more isolated, the former >200 km east of both *raglessi* and *curnamona*, with the Strzelecki Desert intervening, and the latter on the opposite side of the Murray-Darling basin, another 500 km further east.

Relatively slight but statistically significant differences in morphology, plumage and mitochondrial DNA permit the identification of seven subspecies within Thick-billed Grasswren. One, the population given an informal epithet 'eyre', was previously undescribed and unnamed.

Amytornis modestus cowarie subsp. nov.

Holotype.—Adult male, SAMA B56067, collected and prepared by L. P. Pedler, near Karakaranthina Creek, c.12 km east of Cowarie Homestead, north-eastern South Australia (27°42.0'S, 138°25.85'E), on 24 September 2008. Mass 20 g, wing (max. flattened chord) 58 mm, tail (central rectrix from emergence to tip) 72.3 mm, bill length (from skull to tip) 11.7 mm, bill depth (at level of frontal feathering) 6.1 mm.

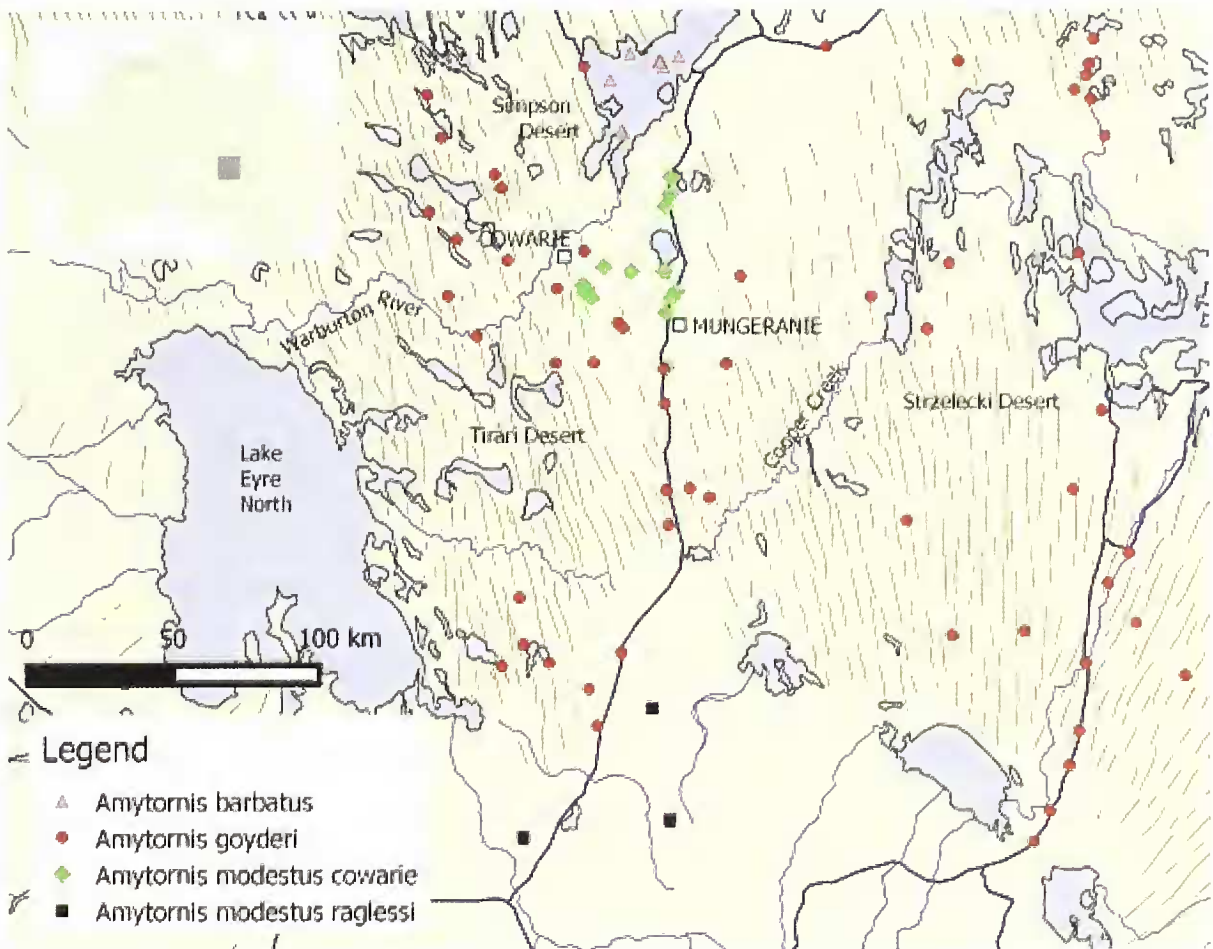


Figure 7. Map of north-eastern South Australia east of Lake Eyre, showing localities of all known records of the newly described *Amytornis modestus cowarie*. Also shown are immediately surrounding records of Eyrean Grasswren *A. goyderi* and Grey Grasswren *A. barbatus*, as well as the three northernmost records of *A. modestus raglessi*.

Paratype.—Adult female, SAMA B56235, collected and prepared by L. P. Pedler, near Birdsville Track, Cowarie Station, c.25 km north of Mungering Homestead, north-eastern South Australia (27°48.0'S, 138°43.6'E), on 26 October 2009. Mass 17 g (nematode infestation), wing 60 mm, tail 67.8 mm, bill length 11.7 mm, bill depth 5.6 mm.

Plumage description of holotype.—Colour assessment is based on Smithe (1975), following D. I. Rogers and K. Bartram (*in* Higgins *et al.* 2001: 442–443) for their descriptions of *A. m. indulkanna* and *A. m. raglessi* (given as *A. textilis modestus*). Centre of frons and crown dark (hair) brown (119A), each feather becoming paler towards the edge, with off-white shaft-streaks (paler than drab grey / pale horn 119D/92). Rest of crown, nape and back and sides of neck much paler (light drab / drab grey 119C/D) with similarly paler feather edges and off white shaft-streaks. Small area of side of frons and upper lores forms subtly tinted fore-supercilium (Yellow ochre 123C). Lower lores, face, ear-coverts dark to light drab (119B/C) with feather edges and shaft-streaks (as above) prominent, producing a distinctly streaked effect. Chin and throat nearly as pale as the off-white shaft-streaks (pale 119D/92) rendering the latter almost imperceptible. Mantle and scapulars grading between pale back of neck (119C/D) and slightly darker back, rump and uppertail-coverts (119B/C). Upper breast as throat, lower breast, belly and vent similar (pale 119D/92) but unstreaked. Tibial feathers and flanks pale buff (119C/D / tawny olive 223D). Uppertail dark drab (119B) with pale fringes (119D / 223D). Undertail light drab (119C) with similarly pale fringes.

Upperwing-coverts light drab (119C), remiges darker (119B/C) with similar pale edges. Bases to outer webs of inner primaries subtly tinted (Yellow ochre (123C) forming patch at base of primaries on folded wing.

Variation.—Of five specimens, there is slight variation in the depth of tone and in the extent of pale buff coloration on the flanks. The paratype bears the hallmark of females of the species, an irregular bright tawny (38) patch on the lower breast-sides / flanks.

Diagnosis.—This restricted-range subspecies is (with *A. m. obscurior*) the palest and is the least streaked ventrally of all, and is included in a phylogroup of four that is genetically divergent from *A. m. modestus* and from *A. m. indulkanna*. It is readily distinguished from the dark, heavily streaked and long-tailed, far eastern *A. m. inexpectatus* that is unsampled molecularly. Within its own phylogroup, it has a shorter tail (mean 72.9 mm, range 70.6–76.5 mm) than *A. m. obscurior* (80 mm for the only male specimen) and *A. m. curnamona* (mean 78.1 mm, range 77.6–78.8 mm), but only relatively shorter than *A. m. raglessi* (mean 74.5 mm, range 69.3–77.8 mm), from which it is distinguished by shorter bill and wing measurements, more lightly streaked underparts and paler plumage.

Etymology.—Named for the pastoral property Cowarie Station, which harbours almost its entire known population and which itself is named after a small locally occurring carnivorous marsupial, the Kowari *Dasymroides byrnei*. The name is that of the Dieri people of the region, in earlier orthography rendered Kau-ri by the Lutheran missionaries, Homann and Koch in their 1870 'primer' (H. Kneebone pers. comm.) and as Cowirrie by Gason (1879).

Distribution.—Known only from stony rangelands of the southern (and major portion) of the Sturt Stony Desert, to which it is confined by the surrounding sand dunes of the Simpson, Tirari and Strzelecki Deserts in the west, south and east, respectively, and by the Warburton River floodplain in the north. The sand dune deserts named above provide the particular habitat requirements of Eyrean Grasswrens *A. goyderi* and the Warburton floodplain likewise supports Grey Grasswrens *A. barbatns diamantina*. The nearest conspecific population, *A. m. raglessi*, is present in similar stony rangelands to the south, beyond the Tirari Desert and Cooper Creek floodplain, its closest known locality being c.110 km from the southernmost record of *A. m. cowarie* near Mungeranie (Fig. 7).

Conservation status.—The known Extent of Occurrence (EOO) of this subspecies is <1,500 km². Among other subspecies, the Area of Occupation (AOO) has been estimated to be no greater than 4% of the EOO (Garnett *et al.* 2011), which would translate into <60 km² AOO for the new subspecies. Population density is probably similar to that of *A. m. indulkanna*, which is estimated at four adults/km² (AB pers. data) and the total population of *A. m. cowarie* therefore probably numbers fewer than 1,000 mature individuals. The above data indicate a conservation status of Vulnerable (IUCN 2012).

Summary of subspecific divisions in *Amytornis modestus*

Conservation status is provided, as assessed by Garnett *et al.* (2011), applying contemporary IUCN criteria.

A. m. modestus

Extinct. Long-tailed, darker dorsally but very lightly streaked below. Unique habitat.

A. m. indulkanna

Least Concern. Pale and lightly streaked, very short-tailed. Genetically distinct from *A. m. modestus*, but in the same western clade.

A. m. raglessi

Vulnerable. Similar to the previous subspecies but slightly longer tailed and genetically divergent, within a separate eastern clade.

A. m. cowarie

Not assessed by Garnett *et al.* (2011) but Vulnerable if same criteria applied. The palest subspecies of all, relatively short-billed and short-winged.

A. m. curnamoua

Near Threatened. The darkest and most heavily streaked within the eastern clade, longer tailed than *A. m. raglessi* and *A. m. cowarie*.

A. m. obscurior

Critically Endangered. Perhaps the longest-tailed within the eastern clade and paler than all but *A. m. cowarie*.

A. m. inexpectatus

Extinct. The longest-tailed subspecies, relatively slender billed, dark and heavily streaked.

Acknowledgements

I am deeply indebted to Graham Carpenter and Lynn Pedler for their exceptional field skills in finding grasswrens and doubly to Lynn for his perseverance and labour in obtaining and preparing the fine study skins that underpin this analysis of diversity within the species. Philippa Horton, Leo Joseph and Les Christidis have encouraged my interest in the genus over many years, and I am grateful to Nate Rice, Academy of Natural Sciences Philadelphia, Paul Sweet and Mary LeCroy, American Museum of Natural History, New York, and Steven van der Mije, Naturalis Biodiversity Center, Leiden, for access to their collections. I also acknowledge the support and interest of Sharon Oldfield and her family, owners and managers of Cowarie Station. Heidi Kneebone advised me on Dieri names, Terry Reardon produced the statistical analysis and Jeremy Austin and Brian Blaylock prepared the maps, one modified from Margaret Cawsey. I thank them all. Eleanor Russell and Dick Schodde, as well as the editor and an anonymous reviewer, suggested helpful amendments to the submitted manuscript. Nomenclature in this paper was reviewed by the Working Group on Avian Nomenclature of the International Ornithologists' Union.

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